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Ontogenetic Change in the Radula of the Gastropod *Epitonium billeeana* (Prosobranchia: Epitoniidae)

by

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Abstract. *Epitonium billeeana* (DuShane & Bratcher, 1965) is identified and described from the Great Barrier Reef, Australia. Like other epitoniids, *E. billeeana* was found to be a protandric hermaphrodite, changing sex between 8.6 and 12.7 mm shell length. Middle lateral radular teeth change within a particular row with growth, from a relatively small denticulate structure to a larger smooth structure. Transitional radulae are identified. We suggest the radula change is mediated or instigated by the change from the male to the female reproductive state.

INTRODUCTION

One of us (A.J.P.) is currently investigating the ecology of coral eating gastropods on Australia's Great Barrier Reef. A thin-shelled wentletrap is moderately abundant on middle- and outer-shelf coral reefs where it is obligately associated with scleractinian corals belonging to the family Dendrophylliidae. Not only does this epitoniid feed exclusively on two particular species of dendrophylliid coral, but the animal also resembles these host corals by being vivid golden-yellow in color; such pigmentation is an outstanding exception for a family whose other members are all generally white. This distinctive epitoniid has been known from Australia as the "golden wentletrap" for a decade and figured in color in several publications (MacLeish, 1973; Coleman, 1978, 1981; Endean, 1982; Rudman, 1984) but no specific name has been attached to it. We show here it is referable to an eastern Pacific taxon, *Epitonium billeeana* (DuShane & Bratcher, 1965). The species' full range extends, in tropical waters, throughout the Pacific and across the Indian Ocean to the Maldive Islands.

In the course of studying the gut of *Epitonium billeeana,* we made the unexpected discovery that an ontogenetic change takes place in the shape of teeth within rows of its radula. The purpose of this paper is to document this significant change, which has not been hitherto suspected in the Epitoniidae.

The ptenoglossan radula of epitoniids bears similar, elongate teeth with or without denticles on the blade (Thiele, 1928). As with most other gastropods possessing a multiseriate radula, numbers of teeth and tooth size increase with an individual's growth (Thompson, 1958; Bertsch, 1976). Most species of epitoniids whose radulae have been studied possess denticles (Thiele, 1928; Clench & Turner, 1952; Taki, 1956, 1957; DuShane & Bratcher, 1965; DuShane, 1974, 1979). None of these authors reports any alteration in the presence of denticles with growth in any species, so tooth shape has been assumed to be invariable and hence specifically diagnostic, as for most other gastropods (Fretter & Graham, 1962). Here we report one clear instance where this is not the case. We show that the teeth of *Epitonium billeeana* change in shape within an individual as it grows.

MATERIALS AND METHODS

Epitonium billeeana was collected from its host corals, *Dendrophyllia gracilis* Milne Edwards & Haime and *Tubastrea faulkneri* Wells in 6 to 16 m on Heron and Wistari reefs (23°27'S, 151°55'E) at the southern end of the Great Barrier Reef in Queensland, Australia, in September 1984 and September 1985. Twenty-six specimens from 4.8 to 23.6 mm shell length were collected specifically to examine their radulae. All were fixed in Bouin's solution, which decalcified the thin shells in three days. The gonad was sectioned (6 μm) to determine sex and sections were stained using Mayer's hematoxylin and 0.3% alcoholic eosin (Luna, 1968).

Two methods were used to prepare radulae for light microscopy. In one, the pharyngeal mass was excised and heated in 10% KOH at 100°C for 20 min. The isolated radula was then rinsed in distilled water, blotted dry, stained in acidic fuchsin (1 h), rinsed briefly (30 sec), and mounted

Figure 1

Epitonium billeeana, SEMs of shell. A. Whole shell (length = 4.9 mm). B. Protoconch (bar = 0.5 mm). C. Detail of sculpture (bar = 100 μm).

in polyvinyl-alcohol-lactophenol (PVA). The second method followed MIKKELSEN (1985). The excised pharyngeal mass was placed in a marked well of a multi-well Boener slide in 10% KOH at room temperature (20–27°C) for 24 h. The isolated radula was then stained briefly (approximately 5 min) in acidic fuchsin before mounting in carboxymethyl-cellulose (CMC). For light microscopy, best results were obtained following the techniques outlined by MIKKELSEN (1985), except for larger radulae, which were mounted in PVA which necessitated longer staining (1 h) in acidic fuchsin. The more viscous PVA medium gave greater control in manipulating radulae while they were being mounted.

Radulae to be examined by the scanning electron microscope (SEM) were placed individually in small vials of distilled water and ultrasonicated for 20 sec. Some were attached to the flat surface of pin-type SEM stubs with double-sided adhesive tape. In other preparations, copper paint was dabbed onto the stub (to create an elevation on the surface) and allowed to dry. Then glue from adhesive tape, which had been obtained by brushing the tape with a fine-tipped paint brush dipped in chloroform, was used to attach the radulae to the paint spots. This latter technique produced better results in that relatively more radular teeth were available for examination.

All measurements of teeth were made with a calibrated

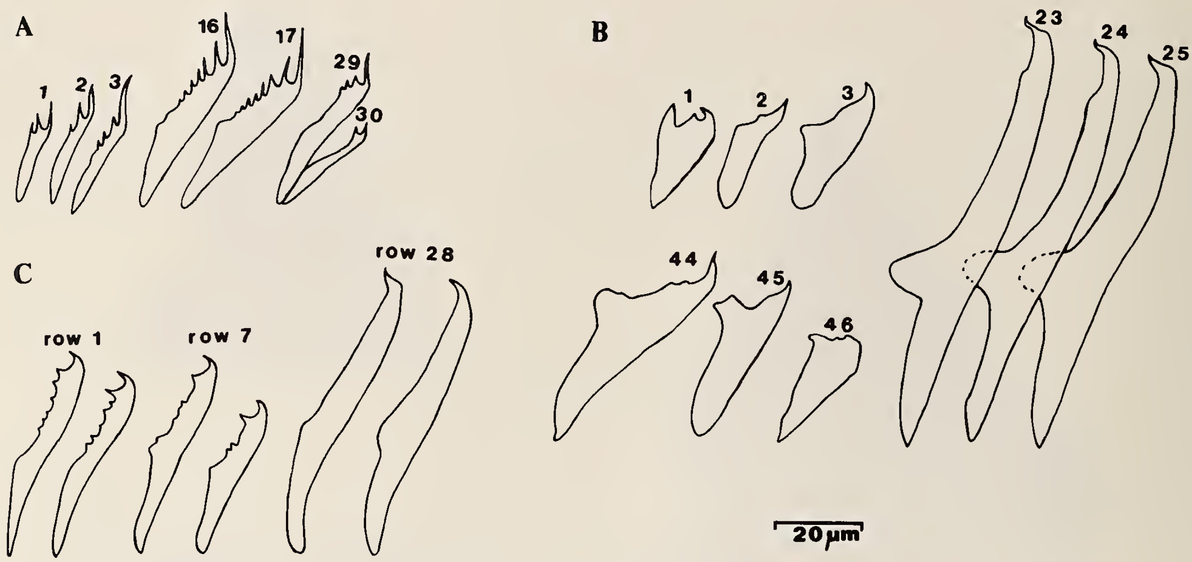

Figure 2

Epitonium billeeana, radular teeth. A. Inner laterals (tooth numbers 1–3 counting outwards from the midline), middle laterals (16, 17), outer laterals (29, 30), shell length = 6.4 mm. B. Inner laterals (1–3), middle laterals (23–25), outer laterals (44–46), shell length = 23.6 mm. C. Middle lateral teeth from anterior (row 1) to posterior (row 28) tooth rows, shell length = 9.9 mm.

eye piece and drawings made with the use of a camera lucida.

TAXONOMY

Epitonium billeeana (DuShane & Bratcher) is a distinctive epitoniid because of its shell sculpture, animal pigmentation, and habit of living obligately with dendrophylliid corals. It was first described from the Gulf of California (DuShane & Bratcher, 1965) and is currently recognized as being widespread in the Panamic Province of the eastern Pacific Ocean (DuShane, 1967, 1974; Keen, 1971). Specimens from the eastern Pacific are identical with western Pacific and eastern Indian Ocean material, and we have no hesitation in identifying them as *E. billeeana.* Robertson & Schutt (1984) provisionally applied this name to Indo-Pacific populations of the "golden wentletrap."

It is desirable to give a full synonymy so researchers can consult literature on this species without being confused by the different names that have been applied in different countries.

Synonymy

Scalina (*Ferminoscala*) *billeeana* DuShane & Bratcher, 1965: 160–161, pl. 24, figs. 1–4; DuShane & Poorman, 1967: 424.

Epitonium (*Asperiscala*) *billeeana* (DuShane & Bratcher): DuShane, 1967:87; DuShane & McLean, 1968:1, 2, fig. 1.

Epitonium billeeana (DuShane & Bratcher): Robertson, 1970:45.

Epitonium (*Asperiscala*) *billeeanum* [*sic*] (DuShane & Bratcher): Keen, 1971:424, fig. 612; DuShane, 1974:9, 10, figs. 13, 15, 155a, 155b; Robertson & Schutt, 1984: 1, 4.

Epitonium sp.: MacLeish, 1973:755 (photograph by V. Taylor); Coleman, 1978:116; Coleman, 1981:13, 44; Endean, 1982:138, fig. 137; Rudman, 1984:172.

Epitonium sp. 5: Loch, 1982:5, illust.

We share DuShane & Bratcher's (1965) and Robertson & Schutt's (1984) uncertainty that *Epitonium* is really the most appropriate genus-level taxon to accommodate *Scalina billeeana.* The species does seem incongruous in that genus, but is more suitable there than in *Amaea* or *Cirsotrema.* Proper generic allocation must await a phylogenetic analysis of the entire family. The specific name, *billeeana,* is a patronym honoring Ms. Billee Dilworth. As such it is a non-Latin noun in apposition and hence indeclinable, *i.e.,* its termination cannot be changed to agree in gender with the generic name ("*billeeanum*" is thus incorrect in the combination *Epitonium billeeanum,* even though the gender of the Latin genus *Epitonium* is neuter).

Description

The following brief description distinguishes *Epitonium billeeana* from other, sympatric, Indo-Pacific congeners.

Shell (Figure 1A) to 25 mm in height. Protoconch (Figure 1B) high and conical, multispiral (3–4 whorled),

Figure 3

Epitonium billeeana, SEMs of radular teeth and coral spirocyst tubes. A. Denticulate middle lateral teeth, shell length = 6.0 mm, bar = 10 μm. B. Smooth middle lateral teeth, shell length = 21.3 mm, bar = 10 μm. C. Teeth with undischarged coral spirocyst tubes, shell length = 12 mm, bar = 10 μm. D. Detail of spirocyst tube from C, bar = 1 μm.

possessing faint, opisthocline axial ridges, dull purple in color. Teleoconch elongate, possessing 7 or 8, thin, globose, strongly convex whorls when full grown; sutures deeply impressed; sculpture reticulate, consisting of equal, low, rounded, spiral cords (12–15 on body whorl) that are overridden by numerous (60–130 on body whorl), sharp, axial ridges (Figure 1C) each ridge elevated into a lamella where it crosses a spiral cord; sculpture weaker on body whorl of adults, spiral cords predominating; color white, with a purplish hue extending to 4th teleoconch whorl as a thin median stripe; overlain by a thin, adherent, pale buff periostracum. Aperture circular, peristome vertical with a moderate anterior expansion. Shell umbilicate. Head-foot, mantle and visceral mass of animal chrome-yellow; showing everywhere through the shell in life.

SEXUALITY

Like other wentletraps (Robertson, 1981; Boss, 1982; Melone, 1986), *Epitonium billeeana* is a protandric her-

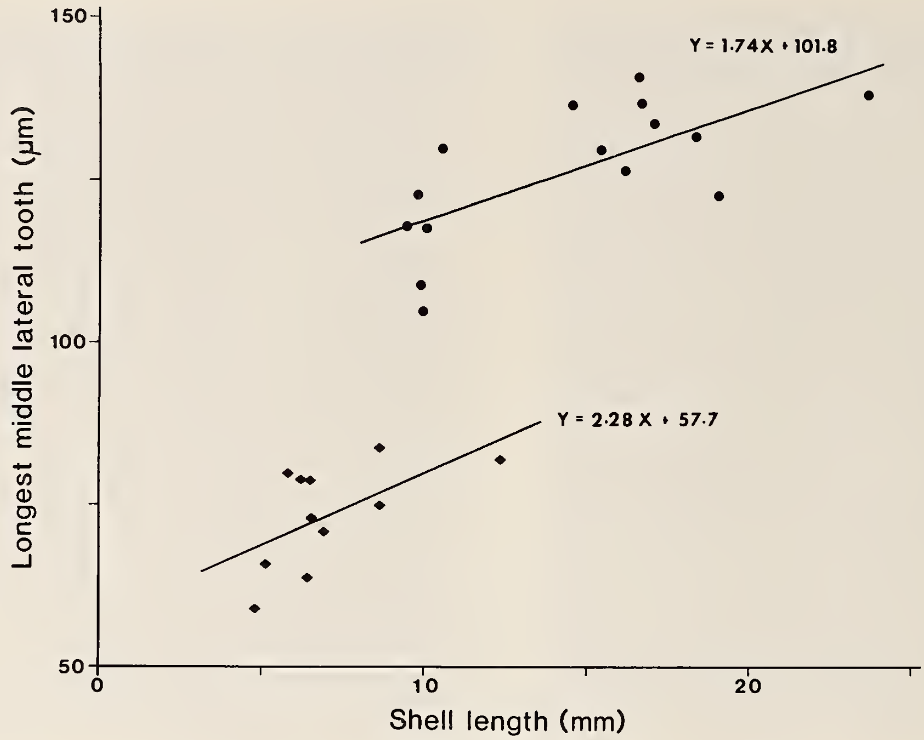

Figure 4

Epitonium billeeana, relationships between shell length and the length of the longest middle lateral tooth. (◆) Denticulate teeth, regression line Y = 2.28X + 57.7, $r = 0.596$, $P < 0.1$. (●) Smooth teeth, regression line Y = 1.74X + 101.8, $r = 0.698$, $P < 0.05$.

maphrodite. Based on our own observations on the state of the gonad, males (with shell lengths from 4.8 to 12.3 mm) are generally smaller than females (8.6 to 23.6 mm). Mature and developing spermatozeugmata and spermatozoa (as figured by NISHIWAKI [1964], TOCHIMOTO [1967], and NISHIWAKI & TOCHIMOTO [1969]) were observed in the testes of males and mature and developing ova were present in the ovaries of females. When sampled, all females were identifiable by the presence of strings of egg capsules.

RADULA DESCRIPTION

Epitoniids have a ptenoglossan radula, a broad structure that possesses many lateral teeth but lacks a rachidian (GRAHAM, 1965; BOSS, 1982). Within the radula, each row consists of two symmetrical halves. In that of *Epitonium billeeana,* the inner laterals of every half row (*i.e.,* those teeth nearest the midline) are smallest. Moving outwards, tooth size gradually increases to a maximum about halfway along each half row. Beyond this point, tooth size gradually decreases to the point where the outer laterals are only slightly longer than the inner ones. Teeth of every half row can thus be divided into three groups—inner, middle, and outer laterals (Figures 2A, B). Similar changes in relative tooth size across a half row have been noted in some of the epitoniids examined by CLENCH & TURNER (1952) and TAKI (1956, 1957). TAKI (1956) even segregated the teeth of *E. latifasciatum* (Sowerby) into three regions—inner, middle, and outer. All the teeth of *E. billeeana* terminate with a single, pointed cusp and below the cusp there may be up to seven prominent denticles along the blade. The cusp is always larger than any of the denticles. When a tooth possesses more than one denticle, that immediately below the cusp exceeds all the others in length (Figure 3A).

The radula of epitoniids covers the entire surface of the odontophore, which is divided into halves by a deep, mid-dorsal, longitudinal groove (GRAHAM, 1965). Consequently radulae are extremely difficult to mount flat and radular formulae are often difficult to determine precisely. For this reason, it was only possible to count the numbers of lateral teeth accurately in three radular preparations of *Epitonium billeeana.* These, together with the length of each specimen's shell in parentheses, are as follows: 30 × 30.0.30 (6.4 mm); 39 × 40.0.40 (8.6 mm); 57 × 62.0.62 (15.9 mm).

ONTOGENETIC CHANGE

The large middle lateral teeth exhibit the greatest degree of change with growth of an individual. The middle lateral teeth of small *Epitonium billeeana* differ from those of large *E. billeeana* in size and the presence or absence of denticles

(Figure 4). Small specimens of *E. billeeana* (<8.6 mm) were found to have comparatively small (average length of longest middle lateral tooth 71 μm), denticulate (3–7 denticles), middle lateral teeth (Figures 3A, C). Large *E. billeeana* (>12.3 mm) were found to have longer (average length of longest middle lateral tooth 133 μm), smooth, middle lateral teeth (Figure 3B). Wentletraps of intermediate size (8.6–12.3 mm) were found to have middle lateral teeth of intermediate size (average length of longest middle lateral tooth 105 μm) which were either denticulate (1–7 denticles) or smooth. *Epitonium billeeana* of intermediate size with smooth middle lateral teeth also possess at least some denticulate middle laterals at the anterior end of their radula. In these cases (six examined) the oldest middle lateral teeth are always denticulate and smaller than the smooth, more recently formed middle lateral ones nearer the germinal epithelium (Figure 2C). These radulae are in transition between possessing relatively small, denticulate and longer, smooth middle lateral teeth. The occurrence of transitional radulae in *E. billeeana* of intermediate size demonstrates the change in tooth morphology with ontogeny. Table 1 correlates the ontogenetic changes of tooth morphology with sex in *E. billeeana*.

Through the courtesy of Mr. I. Loch of The Australian Museum, Sydney, we were able to examine SEMs of radular teeth and the protoconch of a specimen from Christmas Island, eastern Indian Ocean. These characters are in agreement (in size and shape) with those described here for *Epitonium billeeana*. Some of the teeth even have what appear to be atrophied denticles indicating that they may have come from a transitional radula. Unfortunately the shell length of this Christmas Island specimen is not available.

The results presented here are at odds with DuShane & Bratcher's (1965) description of the radular teeth of *Epitonium billeeana*. Many of the radular teeth of their 7-mm specimen were figured as smooth or possessing only a single denticle (DuShane & Bratcher, 1965:pl. 24). From our results (Figure 4), we would predict that all the teeth of such a small individual should be denticulate. This contradiction can perhaps be resolved by ontogenetic studies of the radulae of eastern Pacific material.

DISCUSSION

Reports of ontogenetic change in tooth morphology between rows in gastropod radulae are appearing more and more frequently. Several authors have demonstrated that the number of teeth within a half row increases as the individual grows (*e.g.*, Sterki, 1893; Bertsch, 1976; Robertson, 1985). Beyond this simple allometric increase, there are a few reports like this one of ours of alteration in tooth morphology within a particular row with growth. Sterki (1893) first described such changes in the shape of teeth in some pulmonates, and Carriker (1943) and Hollister (1954) observed that the pattern of denticulation of some prosobranchs' teeth depended on the size of the snail. McLean & Nybakken (1979) and

Table 1

Epitonium billeeana. Changes in sex and radular tooth morphology with growth of 26 specimens.

Shell length (mm)	Sex	Number of specimens	Radula description
<8.6	male	8	All teeth denticulate; 1–3 denticles on inner laterals, 3–7 on middle laterals, 1–5 on outer laterals.
8.6–12.3	male or female	9	As above, or with smooth middle lateral teeth posteriorly and at least some denticulate middle laterals anteriorly.
>12.3	female	9	Middle lateral teeth smooth; inner and outer laterals may be denticulate (1 or 2 denticles).

Nybakken (1970, 1981) reported that several species of *Conus* changed their radula morphology with growth. Hickman (1980) discovered ontogenetic change within rows in the radula of *Hipponix conicus* (Schumacher). Thompson & Brown (1984:11–17) described a "dental metamorphosis" in the opisthobranchs *Tritonia hombergi* Cuvier and *T. plebeia* Johnston wherein juveniles have denticulate lateral teeth and adults have completely smooth laterals. The rachidian teeth of several muricids alter with growth (Fujioka, 1982, 1984a, b, 1985); for example, those of *Morula margariticola* (Broderip) change from pentacuspidate to tricuspidate (Fujioka, 1984b). Most recently has come the finding that denticulation of the "pseudocentral" tooth in the radula of *Tricolia variabilis* (Pease) also changes with growth (Robertson, 1985). All these reports indicate that the phenomenon of ontogenetic change in tooth morphology within particular rows may be more widespread in the Gastropoda than previously suspected.

The most vexing question—what causes this alteration—remains. Dietary change or sexual dimorphism seem to be the two most probable explanations, yet neither appears, at the present time, to offer a satisfactory answer for the observations. Our data on *Epitonium billeeana* present some challenges to both these hypotheses. Hickman (1980) and Nybakken (1981) attributed changes in tooth morphology to differing juvenile and adult diets. In the case of *E. billeeana*, small and large individuals occur, often side by side, on exactly the same coral and they apparently exhibit the same feeding behavior. Other evidence correlates differing radular morphologies with the sex of an individual; for example, the radula of male *Drupella* species and *Tricolia variabilis* changes from a female-like state in juveniles to the male state with sexual maturity (Fujioka, 1982; Robertson, 1985 respectively). Our observations on *E. billeeana* indicate the radular change may be sexually mediated, or at least instigated, but individuals apparently switch sex from male to female before the radular change is completed. The reason for the divergence of radular tooth morphology between sexes, in both dioecious and protandric hermaphrodite gastropods, may ultimately be shown to be related to feeding efficiency and, hence, the energy requirements of the sexually reproducing female individual.

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